Theta and alpha oscillations: Dependency on navigation tasks

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1 Introduction

Rhythmic Slow Activity, or theta rhythm, consisting of 4-12 Hz oscillations, is the dominant rhythmic neuronal activity in lower mammals. Perhaps the best known aspect of this type of oscillation is its relationship to encoding and retrieval of spatial information in rodents. The activity of so-called "place cells" in the hippocampal formations of freely moving rats depends strongly on the specific location of the animal in its environment [1]. In humans, however, theta activity is less prominent. It occupies a narrower frequency band (4-7 Hz) and generally is dominated by the alpha rhythm. Whether there exists a relationship between theta oscillations and the processing of spatial information in humans, as in lower mammals, has not been clearly established. Using magnetoencephalography (MEG), a noninvasive functional brain imaging technique with high temporal resolution, we show here that the performance of a navigational task is associated with a strong increase in theta activity.

This work follows a recent study by Kahana *et al* [2], who recorded EEG during surgery from subdural electrodes implanted in three epileptic patients as they navigated through 6-turn and 12-turn virtual reality mazes. They found that for the longer maze theta power was significantly greater and the length of theta bursts was significantly longer. During navigation theta rhythm was present in widely separated cortical regions, including temporal and parietal cortex.

Encouraged by this result, we decided to implement a similar protocol using MEG. This would allow study of normal subjects under ordinary laboratory conditions. Among the main advantages of such a study is the ability to extend the duration of the sessions to include appropriate control measurements. Signals can also be mapped over the same brain region in each subject to facilitate intersubject comparisons. In the study of Kahana *et al.* clinical considerations determined the extent and placement of the electrode grid, and undoubtedly limited the duration of the recording sessions. We also chose to use a different navigational task than the one used by Kahana *et al.* One interpretation of their results is that the increased theta power for the longer maze is the result of increased memory load or increased task difficulty [3], and is not related to navigation *per se*. We therefore sought to maintain memory load constant throughout the task and to compare theta activity between periods when the subject was navigating and periods when he was not. Lastly, in preliminary studies using mazes, subjects often reported difficulty orienting due to the absence of landmarks. We therefore decided to use a virtual reality city (Fig. 1), which simulates a commonplace environment and allows the subject to more easily build an internal representation of the environment.

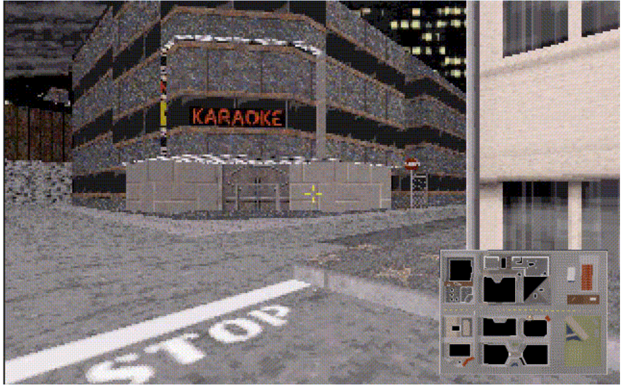


Figure 1: *View of a landmark within the virtual reality city. An overview of the city is shown in the inset.*

2 Methods

The subjects were 11 normal young adults (9 male, two female; 10 right-handed, 1 left-handed) of mean age 28.8 years.

The recordings were made with a 74-channel first-order gradiometer (Magnes II, Biomagnetic Technologies, Inc.) housed within a high-magnetic permeability shielded room. The virtual reality city was built using commercial software (Duke Nuken 3D; Fig.1). The town consisted of two main avenues and 10 secondary streets. Distinctive buildings were placed in strategic locations, such as corners, to serve as reference points.

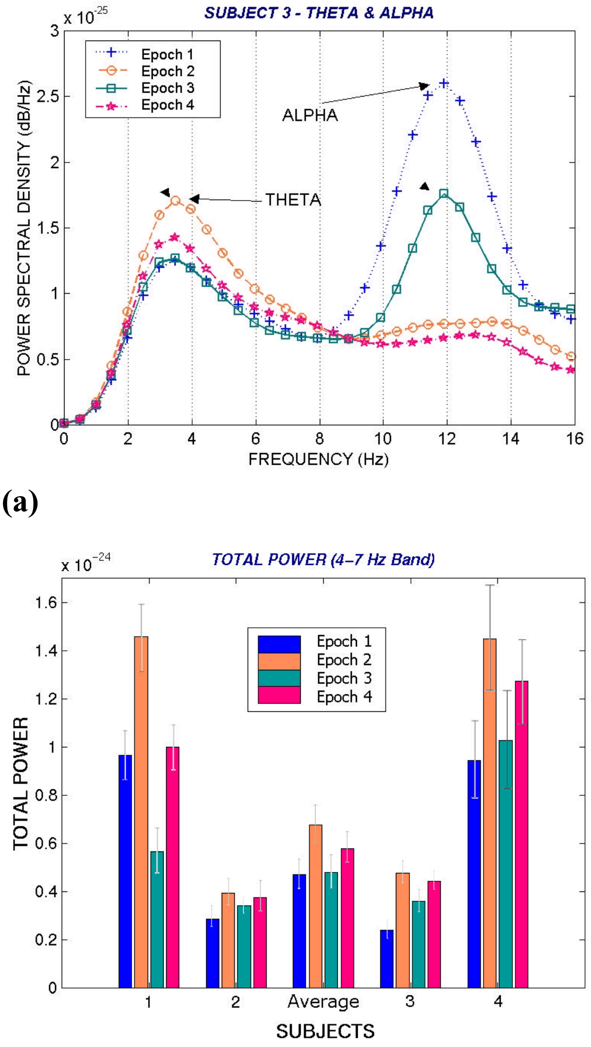
By design, the level of difficulty of the navigational task and the complexity of the virtual reality city were not high. This allowed all subjects to complete the task in a similar amount of time and facilitated comparisons between subjects.

The subjects lay on their sides throughout the measurement. The probes were positioned bilaterally over the temporal regions and were not repositioned during the session. Using a mouse to navigate, subjects were first allowed to explore freely on their own in order to build an internal representation of the city. They were shown the starting point and destination, the locations of the four possible obstructions, and detours from each obstruction to the destination.

At the start of each run, the subjects viewed a static scene of the starting point while awaiting a visual signal to begin navigation. The MEG was recorded continuously, beginning from prior to the start of navigation until the time when the subject arrived at the destination. Four runs were acquired from each subject. The subjects were asked to navigate from the same starting point to the same destination, but in order to reach the destination they would have to navigate around one of several possible obstructions. They were told that they should stop navigating upon encountering the obstruction and that they should visualize a complete detour to the destination. Only then should they resume navigating to the destination. The continuous MEG recording was parsed into four epochs for analysis: a baseline period prior to the start of navigation (epoch 1), navigation from the starting point to the obstruction (epoch 2), suspension of navigation upon encountering the obstruction (epoch 3), and navigation from the obstruction to the destination (epoch 4).

For analysis, each run was divided into four contiguous epochs, as described above. Artifact rejection was performed to remove segments of the recordings contaminated with eye blinks and eye movement artifacts. After bandpass filtering the data from 1-30 Hz, the power spectral density was computed in each epoch and averaged over all channels and all four runs.

In a separate session, three control studies were performed on 4 of the 11 subjects in order to determine whether aspects of the protocol unrelated to navigation could increase theta activity. In the first control study, the subjects were asked to perform two different mathematical calculations that would evoke frontal midline theta activity: counting backwards from 1000 in steps of 7 and computing 2^n for integer n. In the second control study, subjects performed a motor task involving manipulation of a computer mouse. First they traced the lines of a triangle that was displayed on a computer screen. Then they were attempted to trace out a triangle with their eyes closed. . In third control study, subjects passively viewed a tour through a virtual environment similar to the one that they had navigated. A baseline recording was made prior to the performance of each control task.



(a)

(b)

Figure 2: *a) Power spectral density by epoch from 1 subject. The data were averaged over all 37 MEG channels and all 4 runs. Theta peaks were prominent in all subjects; alpha peaks were variable in amplitude. d). Power in the theta band (4-7 Hz) by epoch for four subjects. The grand average, of all 11 subjects, is also presented. Theta power increased markedly when subjects were navigating (epochs 2 and 4), compared with when they were not (epochs 1 and 3).*

3 Results

Figure 2a shows the power spectral densities (PSD) during the four epochs from one representative subjects. The association between theta power and the navigational task was remarkably consistent. All subjects showed large theta peaks near 4 Hz, and in all subjects theta power was greater during navigation (epochs 2 and 4) than during the baseline period (epoch 1) or the suspension of navigation (epoch 3). The percentage of increase of theta power from the baseline period, epoch 1, to the first period of navigation, epoch 2, was 7% or greater in all subjects and averaged 45%. Notice that the peak frequency of the theta oscillations associated with the navigational task was about 3.7 Hz, which is slightly outside the 4-7 Hz frequency band that is commonly associated with theta oscillations. In order to show that the effects reported here could be demonstrated using the conventional definition of theta, the bar graphs of total theta power in Fig. 2b were computed with a 4-7 Hz frequency band. Alpha peaks were prominent in some subjects (Fig. 2a), but were barely visible in others, presumably because the probe was remote from the main sources of alpha in the occipital and posterior parietal regions. In most subjects, alpha desynchronization was seen during navigation, *i.e.*, the amplitude of the PSD in the alpha band was lower during the second and fourth epochs (Fig. 2a).

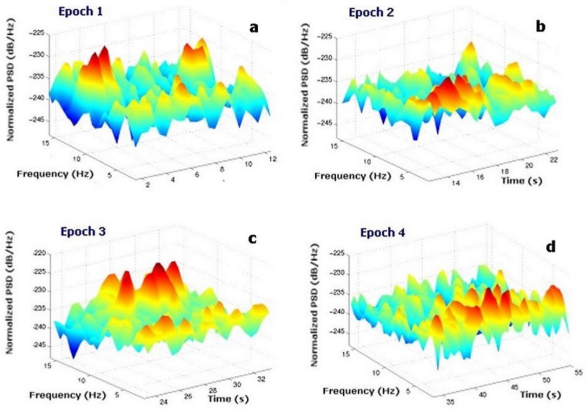


Figure 3. *Time-frequency analysis of the MEG from a representative subject. a-d) The graphs show the data parsed into epochs. Notice that epochs 1 and 3 are dominated by alpha, whereas epochs 2 and 4, corresponding to periods of navigation, are dominated by theta.*

Time-frequency analysis, shown in figure 3, depicts the alternation of theta dominance and alpha dominance throughout a run. The first and third epochs, when subjects were not navigating, were dominated by alpha activity (Fig. 3a,c). In contrast, the second and fourth epochs, when subjects were navigating, were dominated by theta oscillations (Fig. 3b,d). The average duration of theta bursts was approximately 600 msec. No unusually large bursts of theta or alpha were seen; rather, the oscillations were present continually throughout an epoch.

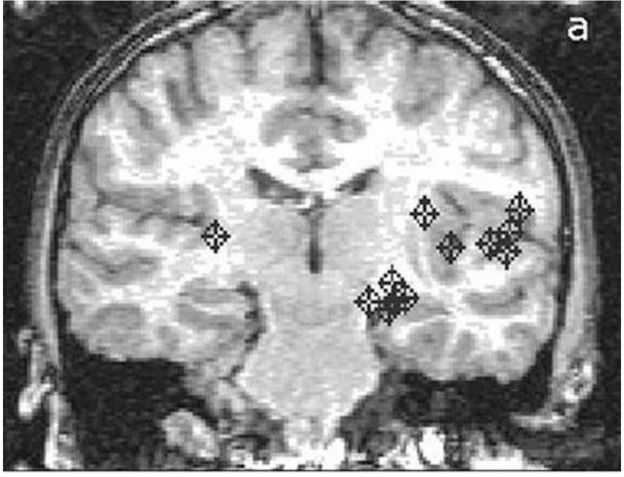


Figure 4. *Localization of dipole clusters from a typical subject, using a single current dipole model. Dipoles cluster along the left superior temporal gyrus (STG) and deep insula; a large deeper cluster lies along the choroid fissure and medial hippocampus.*

Dipole fitting was used to estimate source location at times when the field topography was highly dipolar. Clusters of dipoles were found primarily near the superior temporal gyrus and the deeper temporal structures of both hemispheres (Fig. 4). The time-evolution of the magnetic field topography during periods of large theta oscillations was observed using specialized computer software [4]. The topography implicated source locations mainly in temporal regions, consistent with the dipole fits. In addition to these relatively stationary dipoles, a distinctive spatiotemporal pattern of theta activity appeared repeatedly in the data, in which a dipolar pattern propagated from front-to-back.

4 Discussion

Due to the complexity of the experimental protocol, there are many alternative explanations for the observed increase in theta power, and it is impossible to control for all of them. In our control studies, we attempted to rule out three of the most obvious ones. First, it is well known that various tasks involving mental concentration evoke frontal midline theta [5]. Second, subjects were subjected to complex, streaming visual stimulation as they navigated through the virtual reality environment. Third, navigation required the performance of a precise motor task, consisting of manipulation of a computer mouse. In the first of the control studies, frontal midline theta could be seen at International

10-20 electrode Fz during arithmetic calculation; however no similar increase in theta activity was detected by either of the MEG probes, which were positioned over the temporal regions. In the passive viewing task, the power in the theta band increased slightly, but not nearly enough to account for the large increase seen during navigation. The last control study, involving a motor task, showed no increase in theta power. For all three control studies, the power in the alpha band decreased relative to the resting state.

In designing the task, we attempted to minimize the effects of memory load, attentional demands, and task difficulty. Memory load was thus constant throughout the study. Subjects were required at the beginning to store into memory the paths from the starting point to the destination, including alternate routes, and to retain this information for the duration of the study, which was relatively brief (15 minutes on average). Attentional demands were also relatively constant. Even during the baseline period prior to navigation, subjects were required to be alert for the starting signal. Lastly, the difficulty of the navigational task was made low so that all subjects were able to successfully reach the destination in a similar amount of time and the difference in task difficulty between periods of navigation and other periods was lessened.

A major component of navigation is retrieval of episodic memory, i.e., memory of events that happened at a specific place and time. Some studies support the hypothesis that event related synchronization (ERS) [6] in the theta band has a direct correlation with the retrieval of episodic memory [7]. In our study, however, theta activity was much less during the third epoch, when subjects were attempting to retrieve a map from memory, than during navigation. This suggests that the increase in theta during navigation is due to causes other than the retrieval of episodic memory.

The magnetic field topography associated with the theta oscillations was often highly dipolar, and implicated temporal and parietal sources. In the navigation study of Kahana *et al.*[2] theta oscillations were recorded over many widely separated regions of cortex, including temporal and parietal hemispheres. Functional MRI (fMRI) and PET studies have also demonstrated the participation of several brain regions in navigation protocols, including medial temporal structures, and medial parietal lobe [8]. Thus the topography of the signals detected in this study are compatible with the fMRI and PET findings. More sophisticated MEG source modeling may allow precise comparisons; however, poor knowledge of the relationships between blood flow and metabolism and spontaneous electrical brain activity may preclude meaningful comparisons between our results and those from fMRI and PET studies.

In conclusion, using MEG we demonstrated that theta activity increased strongly while subjects navigated through a virtual reality town. The findings support the hypothesis that theta oscillation and their underlying generators are involved in navigation in normal adult humans, as they are in lower mammals.

Acknowledgements

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References

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